Thesis abstract

Background Finding solutions to the negative impacts caused by weeds in natural systems is a very challenging task for researchers and land managers across the world. Many studies of weed taxa and weed management programmes are often hampered by a lack of knowledge of the basic biology and ecology of these taxa and of the processes and mechanisms contributing to the success of invaders in new habitats. A detailed understanding of the competitive and adaptive attributes of weeds, and the role they play in adaptation to new environments and environmental extremes, remains elusive and incomplete for most species.

In Australia, invasive blackberries of the *Rubus fruticosus* L. aggregate (approximately 15 species, most of which are putatively polyploid) are problematic weeds. Surprisingly, little is known about the biological and ecological attributes of individual species within the aggregate. Control and management programmes are typically structured around the aggregate as a whole and have evolved primarily towards finding solutions to the agricultural threat they pose, often at the expense of testing and expanding our understanding of the complex biology and ecology of blackberries and of the factors that facilitate their invasiveness.

Location Southern Australia and South Australia.

Objectives My research identified and investigated the biological and ecological attributes of individual species of blackberries and their potential for range expansion in southern Australia. I estimated the bioclimatic niches of selected *Rubus* taxa and expand the understanding of some of the biotic and abiotic preferences of these species and their relative ability to invade native vegetation, which helps to explain their invasiveness in Australia. I also examined the competitive impacts of three blackberry species on selected native species.

Methods I used five types of species distribution models (SDM), (in the *Dismo* package of R) and constructed predictive maps of the potential ranges of different species within the *R. fruticosus* agg. in southern Australia and in South Australia, based upon known locations of different species of blackberries combined with a set of bioclimatic variables. I then measured the overlaps and similarities of the climatic niches of the different species using environmental niche modelling techniques (ENM) and tested (using two measures of niche similarity) the statistical significance of observed levels of niche similarity in South Australia, relative to a null hypothesis of random overlap.

In a separate field survey, areas of native vegetation in the Mt. Lofty Ranges region were surveyed for the presence/absence of ten blackberry taxa. I identified five common species that invade native vegetation and developed explanatory generalised linear mixed models (GLMM) to predict the occurrence of the five species based upon abiotic and biotic variables measured at the random field quadrats.

I also measured the growth response of two Australian natives (*Leptospermum continentale* and *Acacia provincialis*) in competition experiments under shade-house conditions and in the field, in which the native plants were planted along with three common blackberry species that invade native vegetation (*Rubus anglocandicans*, *Rubus erythrops*, and *Rubus leucostachys*).

I used flow cytometry methods (FCM) and chromosome counts to assess ploidy level and nuclear DNA content for six blackberry species in their invasive range in Australia using material collected in the Mt. Lofty Ranges. Species in the *Rubus fruticosus* L. aggregate that occur in Australia have been considered likely to be facultatively apomictic and tetraploid with the exception of one diploid taxon.

Findings

Species distribution modelling The maps generated for the blackberry species demonstrated significant variability among the four most common species with respect to their potential invasive ranges. *Rubus anglocandicans* for instance, currently exists over a broad area of southern Australia and has the potential to expand its range primarily at the margins of known populations in all southern states. In contrast, *Rubus erythrops* has a more limited actual range in Victoria, South Australia and Tasmania but my modelling indicates a capacity to expand its range into new areas in Western Australia and New South Wales. Other less common species also display a similar potential.

Environmental niche modelling The climatic niches of seven blackberry species were compared in pair-wise tests using the Hellinger's I_{mod} and Schoener's D statistics by the identity tests and background similarity tests in the ENMTools software package. Niche overlaps were typically less than expected under a null hypothesis of random overlap, demonstrating the presence of niche differentiation with respect to the climatic variables measured. The niche of *R. anglocandicans* was more distinctive than those of the other species of the *R. fruticosus* agg. examined.

Survey of native vegetation Logistic regression analyses of relationships between measured attributes of random survey sites in native vegetation and the occurrence of taxa of

the *R. fruticosus* agg.*,* demonstrated that the presence of different species of blackberries varied as a function of different combinations of variables characteristic of each modelled species. For instance, *R. anglocandicans* occurs in habitats characterised by a broad range of aridity but avoids areas of high sunlight intensity in gaps in native vegetation. The presence of *R. erythrops* appeared partly dependent on gaps in native vegetation, whereas the second most common species *R. leucostachys* showed a very low association with native vegetation appearing to prefer unshaded habitats.

Competition Growth responses of two native plant species - *L. continentale* and *A. provincialis* – were measured when grown under shade house conditions in competition with three blackberry treatments (*Rubus anglocandicans*, *Rubus erythrops* and *Rubus leucostachys*). The results showed highly significant effects on growth of *L. continentale* (for above-ground and below-ground weights of plants (both wet and dry weights with the exception of root dry weight), height increase and stem area increase), after a four-month growth period. Growth responses of *A. provincialis* (considered to be a nitrogen fixer) under shade house conditions showed no significant growth effects of plantings with three blackberry species measured over the same period for the same growth parameters. The overall pattern of effects among blackberry species on the growth of *L. continentale* was consistent over all six metrics measured, showing *R. anglocandicans* has the strongest effect and *R. leucostachys* the weakest on growth of this native species.

Chromosome numbers and flow cytometry Estimated chromosome numbers are reported for six blackberry taxa in their invasive range in Australia using material collected in the Mt. Lofty Ranges. Chromosome counts for five taxa (2n=28) are indicative of tetraploidy and chromosome counts for one taxon (2n=14) are indicative of diploidy. Genome sizes estimated using flow cytometry for the tested group of blackberry species were small (e.g. less than 10 picograms), standardised against *Pisum sativum* L. The evidence from chromosome counts did not provide any evidence that hybridisation is occurring between the related diploid and tetraploid taxa examined as no triploid cytotypes were found.

Main Conclusions
The maps displaying the potential for range expansion by individual species of blackberries showed several blackberries have apparently not yet reached the limit of their ranges in southern Australia. The multiple model approach combined the power of several algorithms to create a suite of comparative predictive distribution maps of individual blackberry species in southern Australia and in South Australia. Predictions of range expansion at the smaller-scale extent of South Australia predicted potential new range

expansions and expansions at the margins of their current distribution for the species examined.

Employing environmental niche modelling (ENM), this study also revealed measurable niche differences that are characteristic of individual species. ENM showed some species were significantly differentiated in terms of their bio-climatic niches, despite the presence of considerable range overlaps.

The results from the ecological survey of the occurrence of blackberries in native vegetation showed individual species displayed a variable tendency to invade native vegetation habitats predicted by a varying suite of abiotic and biotic variables. Results of the glasshouse competition experiment suggest that native plant species that are able to fix atmospheric nitrogen may be more able to compete against some blackberry taxa than species that are not nitrogen fixers. Further field trials are necessary to investigate this possibility.

The survey of variation in chromosome number and DNA content of selected blackberry species in the *Rubus fruticosus* agg. from the Mt. Lofty Ranges indicated that the majority are tetraploid and one is diploid. Further surveys would be interesting to examine the possibility of hybridization among species and to test for further variation in ploidy level.